

ON THE AFFINITIES OF *TRITYLONDON*.

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Tritylodon longævus was described in 1884 by Owen* from an imperfect skull submitted to him by Dr. Exton, the Curator of the Bloemfontein Museum. The specimen is stated to have been found at "Thaba-chou, Basutoland." Unfortunately there is some doubt about this locality, as no place of this name is to be found on any of the recent maps of Basutoland. There is a mountain south of Morija called Thaba-tsueu, which may be the locality. There is, of course, the well-known locality in the Orange River Colony, Thaba'Nchu, but this is hardly likely to be the spot, as Dr. Exton, who submitted the specimen to Owen, was present at the meeting of the Geological Society at which the paper describing the specimen was read, and is not likely to have allowed the statement that the specimen came from Basutoland to have passed without correction, if wrong. It is further highly probable that the name of the locality was given by Dr. Exton, who, of course, would be well aware that Thaba 'Nchu was not part of Basutoland in 1883. The importance of the determination of the locality lies in the fact that the whole of Basutoland belongs to the Stormberg age, and is of much more recent date than the Upper Beaufort beds of Aliwal North and Burghersdorp, which have yielded the Theriodonts. While the latter are believed to be Upper Triassic, the former are most probably Lower Jurassic.

Owen described the specimen as the remains of a Mammal, and pointed out a large number of features which seemed to confirm this view, among others the striking resemblance of the teeth to those of *Stereognathus*; and this view has had the support of a number of

* R. Owen, "On the Skull and Dentition of a Triassic Mammal (*Tritylodon longævus*, Owen) from South Africa." Q.J.G.S., vol. xl., 1884, p. 146.

palæontologists, including Lydekker* and Seeley,† the latter of whom expressed the opinion in 1887 that *Tritylodon* was a “Bunotheroid Rodent.”

In 1894 Seeley,‡ as the result mainly of his discovery of Theriodonts with flattened molar teeth, gave up his earlier view and came to the conclusion that “*Tritylodon* was a Reptile,” but admitted the possibility of its belonging to “a group of animals intermediate between Mammals and Theriodonts.” In 1895 he definitely placed *Tritylodon* in the “Gomphodontia.” As, in 1898, Seeley§ expressed the opinion that the Theriodonts are not the ancestors of the Mammals, we may assume that he has abandoned the view of 1894 that *Tritylodon* may possibly belong to a group intermediate between Mammals and Theriodonts.

Let us look at the evidences which Seeley brings forward in support of the view that *Tritylodon* is a Theriodont and not a Mammal.

In the first place the orbit is said to have been closed behind as in Theriodonts. On this point the specimen gives very little evidence. Owen considered that the orbit was probably incomplete behind, and until a more perfect specimen is discovered it will be impossible to definitely settle the point. As, however, many Mammals have the orbit closed behind by bone the point is not of very much importance. A much more important point is whether *Tritylodon* had a distinct postfrontal or postorbital bone. By Owen the pair of bones behind the frontals are believed to be the parietals; by Seeley they are looked upon as the inner parts of the postfrontals. If they are postfrontals or rather postorbitals they are unlike the postorbitals of the known Theriodonts. In *Gomphognathus* and *Trirachodon* the Theriodonts with which Seeley compares *Tritylodon*, the frontals pass well back between the inner parts of the postorbitals, but in *Tritylodon* the frontals are prevented from passing backwards by the median union of the two bones behind. The bones thus resemble rather mammalian parietals than Theriodont postorbitals. Even, however, should the bones be ultimately proved to be postorbitals, it must be remembered that postorbitals occur in *Ornithorhynchus*.

In the second place Seeley points out that in Theriodonts the snout has a bulbous appearance, owing to the widening of the maxillary bones by the roots of the large canines, while in *Tritylodon*

* R. Lydekker, *Cat. Fossil Mammals*, Brit. Mus.

† H. G. Seeley, “On Parts of the Skeleton of a Mammal, &c.” *Phil. Trans.*, 1888, p. 141.

‡ *Ibid.*, “The Origin of Mammals.” *Int. Cong. Zool.*, Cambridge, 1898.

§ *Ibid.*, “The Reputed Mammals from the Karroo Formation of Cape Colony.” *Phil. Trans.*, 1895, p. 1025.

there is a widening of the snout by the roots of the teeth which have been regarded as the incisors. The facts that the front teeth are separated by an interspace ; that the incisor roots extend into the maxillary bones ; and that in Theriodonts evidences are sometimes apparently found of a successional canine behind the large canine led Seeley to doubt whether the large front teeth in *Tritylodon* "may not be regarded as canines comparable to the canines of Theriodonts, rather than as incisors comparable to the incisor teeth of Mammals like Rodents." The occurrence of an interspace between the front incisors is met with in a number of Mammals, and the fact of the incisor roots extending into the maxillary bone is of such common occurrence in Mammals that it may be said to be the almost invariable rule if the incisors are large. As in no Reptile, Theriodont or other, are large incisor teeth known which pass back into the maxillary bone, the occurrence of them in *Tritylodon* is rather to be regarded as an evidence of the mammalian affinity of the genus. The swelling of the snout, caused by the teeth roots, does not seem to be a character of much importance ; but there is no difficulty in pointing out a number of Mammals in which it occurs—both carnivorous and herbivorous.

Another of Seeley's arguments in favour of the Theriodont affinity, is that "the nares are terminal in *Tritylodon* and in Theriodonts" ; but as the nares are also terminal in Mammals this fact proves nothing. It will be pointed out, however, presently, that the nares in *Tritylodon* are very different from those of the Theriodonts.

Seeley finds another Theriodont character in the posterior nares. He says: "The posterior nares are conditioned as in Theriodonts, opening between the hinder molar teeth. This character is not mammalian. . . . As far as the evidence goes the posterior nares are Theriodont." It is difficult to understand how the conclusion was arrived at that the opening of the posterior nares between the hinder molar teeth is not a mammalian character. Among Rodents—the very Mammals with which Seeley formerly placed *Tritylodon*—it is such a common character that it might be regarded as the rule. But the character is by no means confined to Rodents. It is met with in forms as different in other respects as *Petrogale*, *Procavia*, *Palæomastodon*, *Equus*, *Ovis*, *Coryphodon*, *Uintatherium*, and *Galeopithecus*. In fact, the list of Mammals in which the internal nares open between the posterior molars can be extended to almost any required length, and Mammals fulfilling the condition can be found in most of the orders. It will thus be seen that the position of the posterior nares in *Tritylodon* is similar to that seen in a large number of Mammals. On the other hand, no Theriodont is known

in which the posterior nares open between the hinder molar teeth. Whatever evidence, therefore, is afforded by the position of the posterior nares is in favour of *Tritylodon* being a Mammal rather than a Theriodont.

One character observed by Seeley—the presence of a distinct prefrontal bone—is of much more importance than any of those previously mentioned in determining the affinities of *Tritylodon*. In 1894 he could state, “The presence of a prefrontal bone is a reptilian character unknown among Mammals.” But, in 1896, he discovered that a prefrontal bone exists also in *Ornithorhynchus*, a discovery that has since been confirmed by van Bemmelen.* So that, though the presence of a prefrontal bone would remove *Tritylodon* from the Eutheria or the Metatheria, it would not remove it from the Prototheria.

On the other hand, we have the very important mammalian characters pointed out by Owen. Of these, perhaps the most important is the structure of the molar teeth. The molars have rows of well-developed cusps, and have distinct roots. There is no known Theriodont with either the one or the other, and both characters are found in the molars of known Mammals. There is one important point in connection with the molars, the bearing of which has not, I think, been fully recognised. In 1898 Osborn† pointed out that in “typical Multituberculates like *Tritylodon*” “the dental series are parallel with each other as an adaptation to the forward and backward motion of the jaw.” This conclusion is fully justified. Even if we knew nothing of such animals as *Meniscoëssus* and *Cimolomys*, we could be quite certain from the arrangement of the upper molar cusps that the lower molars must have had the cusps also arranged in rows, and further that the lower molars must have worked against the upper with an antero-posterior movement as in Rodents. To admit of such movement the articulation must have been of the mammalian type, as no antero-posterior movement would be possible in a form having the Theriodont type of articulation; and as the different type of articulation is the only fundamental point of difference between the Theriodont and the Mammal, it follows that *Tritylodon* must have been a Mammal.

The condition of the anterior nares in *Tritylodon* is another point of interest. In all known Theriodonts in which the parts are satisfactorily preserved the premaxillary bones send upwards a median process which meets the nasals and divides the nares. In

* J. F. van Bemmelen, “Der Schädelbau der Monotremen.” Zool. Forschungsreisen in Austr. u.d. Malay Archipel., 1901.

† H. F. Osborn, “The Origin of the Mammalia.” Amer. Nat., May, 1898.

Tritylodon this process is absent, or rather represented by a mere rudiment. In no adult Mammal are the nares ever divided, as in the Theriodonts. In the young Monotremes, however, the median process of the premaxillaries is still seen, and in certain young Marsupials (*e.g.*, *Macropus*) there is a slight trace of it, very similar to that seen in *Tritylodon*. So that any evidence derived from the condition of the anterior nares is also in favour of *Tritylodon* being a Mammal rather than a Theriodont.

Taking all points into consideration, there seems to be no good reason for placing *Tritylodon* with the Theriodonts, and many reasons for leaving it where Owen placed it—among the Mammals. So far as can be made out, the affinities seem to be more with the Monotremes than with the higher forms. It is unfortunate that to-day the only living Prototherians are the extremely degenerate *Ornithorhynchus* and *Echidna*, but it is not improbable that the Multituberculates of Jurassic and Cretaceous rocks may have been Prototherians, and the presence of prefrontal bones would seem to favour this view.

ADDENDUM.

Since the above was written I have received the following information from the Rev. S. S. Dornan, of Morija:—"With reference to your note *re* specimen from Thaba-chou, I know of no locality of that name, or at least of that spelling. I suspect that Thaba-tsueu (pronounced Taba-tswayou) is the correct locality, but the difficulty is that there are several mountains of the same name in Basutoland. There is a Thaba-tsueu about three hours (18 miles) from here, a prominent mountain, but I do not know whether any fossils have been found there or not, though so far as I know the strata are the same as here."

It seems likely that the specimen was collected by some Free Stater who took part in the Basuto war, 1879-81.